

2. UNDER-WATER ILLUMINATION AND ECOLOGY IN TROPICAL ESTUARIES

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LITTLE accurate information is available on the penetration of daylight in the estuaries of tropical rivers. During the cruise of M.Y. "Rosaura" in the winter of 1937-38, surface water samples were collected and brought back to Great Britain for salinity analyses by the Government Chemist. These in some cases proved a matter of difficulty owing to the excessive colour of the water. Since this colour appeared likely to have considerable ecological importance, the Government Chemist kindly returned the water samples to the Plymouth Laboratory where extinction coefficients were determined in the Pulfrich Photometer with nine spectral filters as described by Cooper & Milne (1938, 1939). The extinction coefficient, μ , is defined by the equation

$$\mu d = 2.303 \log_{10} \frac{I_0}{I_1}$$

where d is the length of the column of water measured in metres and I_0 and I_1 are the intensities of light of a given wave-length entering and leaving the water sample. Three months elapsed between collection and the light measurements on 22nd March, 1938, so that there was time for bacterial action considerably to affect the colouring matter. Admixture of salt water may lead to "clumping" or coagulation of colloidal matter.¹ The results are sufficient to show that exceptional opacity existed in the Barima river and in the Demerara river at Georgetown, both in British Guiana (Tables I and II). Blue and green light were even more heavily absorbed than were red and yellow. Data for Neal Point, the most turbid station investigated in the Hamoaze (Tamar Estuary) near Plymouth, England, are included for comparison. If the zone of active photosynthesis be considered as lying

¹ In 1945 extinction coefficients of sea water determined by one of us with the Pulfrich photometer were compared with coefficients determined on "brightness profiles" by an aerial photographic method (Moore, 1947, Table 8). In some cases determinations in the photometer were twice as great. Since no firm explanation was apparent publication has been deferred. Poole & Atkins (unpublished work) have since found a similar discrepancy between extinction coefficients determined with the Pulfrich photometer and those measured in the sea with submarine photometers. It has become clear that the extinction coefficient, measured on a beam of light passing through water enclosed in a tube in a Pulfrich photometer, or probably in any similar visual or photoelectric laboratory absorptiometer, is a very different physical quantity from the vertical extinction coefficient measured by a submarine photometer exposed in the sea or the extinction coefficient determined photographically from brightness profiles. Poole & Atkins explain the discrepancies as due to the forward scattering which they find light to undergo in natural waters. Results with the Pulfrich photometer or any other laboratory absorptiometer employing a beam of light in a tube have value, but they are not the same as those obtained by direct observation at sea or from the air. (Added in proof, 23.ix.53.) There is yet another factor, in addition to the effect of forward scattering from natural waters confined in glass tubes, which Cooper now accepts without reserve. It has been found, following a suggestion of Dr. H. H. Poole, that the geometry of the Pulfrich measuring assembly, as we have used it, makes for an apparent extinction coefficient larger than that obtained by other methods. Comparison with results obtained by Cooper and Milne with the same apparatus is legitimate. Comparison with any other procedure may not be.

TABLE I.—*Hydrographical Data*

Station No.	Name	Date	Position	Depth of river (m.)	State of tide	Surface	
						Salinity (‰)	Temperature (° C.)
38B	Morowhana, Barima River, British Guiana	9.xii.37	8° 15' N., 59° 45' W.	12-20	Ebb	10.90	..
39	Junction of Barima & Arouka Rivers, British Guiana	10.xii.37	2 miles above (south of) Station 38B	20	„	8.3*	26°
40	Demerara River, Georgetown, British Guiana	13.xii.37	..	7	Flood	13.9*	..
47A	Nianimaru, Gambia River	2.i.38	13° 42' N., 14° 58' W.; 120 miles from mouth	9	Ebb	0.00	24°
47B	Nianimaru, Gambia River	3.i.38	13° 42' N., 14° 58' W.; 120 miles from mouth	9	..	0.00	..
48	Tendeba, Gambia River	3.i.38	13° 27' N., 15° 47' W.; 50 miles from mouth	9	1 hr. after high water	2.63	24°

* Salinity is only approximate owing to uncertainty of end-point.

TABLE II

Station No.	Spectral filter number	Centre of gravity of filter (mμ.)	S43	S47	S50	S53	S57	S61	S66.6	S72	S75
			434	463	494	530	572	619	666	729	750
Extinction Coefficients, μ_{pw} as measured with nine spectral filters :											
38B	Morowhana, Barima River		30.7	24.4	19.7	15.6	13.1	10.9	9.4	9.2	10.0
39	Junction of Barima and Arouka Rivers		39.9	30.3	24.8	20.1	16.9	14.3	12.0	11.9	11.1
40	Demerara River, Georgetown		27.2	24.6	23.1	21.4	19.5	19.3	18.5	18.8	23.9
47B	Nianimaru, Gambia River		6.5	5.9	5.25	4.85	4.80	4.45	4.20	5.35	6.1
	Neal Point Buoy, River Tamar, England, low water springs 16.ii.37		18.8	16.5	15.0	14.6	13.4	12.8	—	13.5	12.7
	Ditto, 23.vi.37		6.18	5.48	5.01	4.62	4.63	4.53	—	5.61	6.29
	Neal Point Buoy, River Tamar, England, high water neaps, 17.vi.37		2.11	1.87	1.71	1.58	1.60	1.79	—	3.18	3.86
Depths in metres at which intensity of light is reduced to 1% of that incident on surface (no correction for surface loss) :											
38B	Morowhana, Barima River		0.15	0.19	0.23	0.29	0.35	0.42	0.49	0.50	0.46
39	Junction of Barima and Arouka Rivers		0.12	0.15	0.19	0.23	0.27	0.32	0.39	0.39	0.42
40	Demerara River, Georgetown		0.17	0.19	0.20	0.22	0.24	0.24	0.25	0.24	0.19
47B	Nianimaru, Gambia River		0.71	0.78	0.88	0.95	0.96	1.04	1.10	0.86	0.76
	Neal Point Buoy, River Tamar, England, 16.ii.37		0.24	0.27	0.30	0.30	0.33	0.35	—	0.33	0.35
	Ditto, 23.vi.37		0.72	0.81	0.89	0.96	0.96	0.98	—	0.79	0.71
	„ 17.vi.37		2.10	2.38	2.60	2.81	2.77	2.48	—	1.39	1.15

mainly above the level of 1% illumination (Table III) it must be confined to a layer no more than 40 cm. thick.

Cooper & Milne (1939) found a close relation between the daylight factor and zonation of algae on buoys moored in Plymouth Sound and the Hamoaze. The daylight factors at the boundaries between the algal Zones I and II and between Zones II and III lay at about 80% and 60% respectively. The depths in the tropical estuaries corresponding to these daylight factors are set out in Table IV in which the corresponding Plymouth data are given for comparison. The same distribution of algae is not to be expected in such widely different environments, but even so the daylight factor shows very clearly how greatly the zone of active photosynthesis must be compressed.

The maximum intensity of tropical sunlight is only about 30% greater than that of the brightest summer day in Southern England, but there are two periods with zenithal sunlight each year and the average solar altitude is considerably greater (Atkins, Ball and Poole, 1937). Even so a dearth of phytoplankton and of the animals dependent thereupon might be expected. A comparison with the conditions actually found is thus of interest.

A. BRITISH GUIANA

Station 38: Morowhana, Barima River, 8-9.xii.37

The river is tidal, about 300 metres wide and from 12 to 20 metres deep, and the salinity on the ebb was 10.90‰. The water is apparently sometimes fresher than this, for the local inhabitants are said to drink it. A haul with the 2-foot dredge brought up mud and rotting vegetation, and nothing living except some barnacles (young *Balanus* sp. in the Tetraclita stage) on a stone. The zooplankton, sampled with a silk tow-net (56 meshes to the linear inch), was quite abundant and included the following forms:¹

Pisces: Engraulidae: Larvae under 20 mm.	15
Sciaenidae: " " "	22
Gobiidae: " " "	1
Chaetodipteridae: <i>Chaetodipterus faber</i> (Brouss.)	14 mm.	1
Tetrodontidae: <i>Colomesus psittacus</i> (Schn.)	15 mm.	2
Mollusca: Gastropoda, young,	Several
Crustacea: Decapoda: Sergestidae,	"
<i>Penaeus</i> sp., young	Many
Zoeas,	"
Other larvae,	"
Amphipoda: in tubes,	Several
Isopoda:	2
Copepoda: including <i>Labidocera fluviatilis</i> Dahl	} Many	
<i>Acartia lilljeborgi</i> Giesbr.		
<i>Acartia giesbrechti</i> Dahl.		
Chaetognatha: <i>Sagitta</i> sp., small	Many
Coelenterata: Scyphomedusae: <i>Stomolophus meleagris</i> , young,	3

¹ Such numbers of animals as are given in this paper must be regarded only as indications of relative abundance.

The bulk of the catch consisted of zoeas, copepods and *Sagittae*. The presence of the first two of these groups suggests that some planktonic plant-food must have been present in spite of the low level of under-water illumination.

Station 39 : At the junction of the Barima and Arouka Rivers,
2 miles above Station 38, 10.xii.37

The salinity on the ebb was 8.3‰. The river was remarkably full of fish, many of which must have weighed several pounds. The plankton was here sampled with a 2-m. stramin net (about 16 meshes to the linear inch), streamed from the ship while at anchor. The catch was large but contained no zoeas, copepods or *Sagittae*; these would all have passed through the meshes of the net. The following forms were caught :

Pisces : Engraulidae :	>80
Ariidae : <i>Tachysurus nuchalis</i> (Gunther), 30 mm.	1
Sciaenidae : <i>Stellifer stellifer</i> (Bloch), 10-35 mm.	15
Gobiidae : post-larval, 27 mm.	1
Soleidae : <i>Achirus</i> sp., 23 mm.	1
Cynoglossidae : <i>Symphurus</i> sp., 33 mm.	1
Mugilidae : <i>Mugil</i> sp., 40 mm.	1
Tetrodontidae : <i>Colomesus psittacus</i> (Schn.), 20 mm.	>100
Also several larval fish, unidentified.									
Crustacea : Decapoda : <i>Xiphopenaeus kroyeri</i> (Heller), small	2
<i>Penaeus</i> sp., very small	Many
Sergestidae, young	2
<i>Palaemon</i> sp.	Several
Prawns, not determinable	"
Amphipoda : <i>Pseudoceradocus lutzi</i> Schoemaker	1
Isopoda :	5
Coelenterata : Scyphomedusae : <i>Stomolophus meleagris</i> , adults	5

Station 40 : Demerara River at Georgetown, B.G., 13.xii.37

The river is here about a mile wide and the ship lay only one mile from the open, though very shallow, sea. (There is a depth of only about 8 metres 15 kilometres off shore). The tide ebbs and flows at about 5-6 knots, and on the ebb the salinity was 13.9‰. The water was so turbid that if one's hand was immersed to the wrist the fingers were invisible. The tidal current in 7 metres of water no doubt keeps the water well stirred right down to the bottom. This is suggested also if we compare the extinction coefficients in the Demerara river with those in the neighbouring Barima. Whereas the Barima is strongly coloured brown and shows much the greater absorption in the blue and violet, the Demerara shows a more

uniform absorption through the spectrum, suggesting that a non-selective absorption due to suspended detritus is super-imposed on selective absorption due to brown pigments in true or colloidal solution in the water. (The tidal current in the Barima is less than half that in the Demerara.) The very rapid extinction of under-water illumination must confine active photosynthesis to a very shallow layer. Jenkin (1937) found that the compensation point for *Coscinodiscus excentricus* lay at about 360 lux. This is a mean figure for 24 hours. For the hours of daylight it would be considerably higher. If we take 140 kilolux as a round figure for midday tropical daylight (Atkins, Ball & Poole, 1937) the daylight factor for *Coscinodiscus* would exceed $\frac{0.36}{140} = 0.26\%$. The value 1% for the daylight factor over 24 hours is therefore about as near as we can get at present. Reflection losses at the surface may also reduce the incident light by 4 to 15% according to the degree of roughness. Moreover land plants, and no doubt marine algal also, differ greatly in their response to light. Even so, under the most favourable conditions the depth of the layer of active photosynthesis could not have exceeded one-third of a metre, but nevertheless, the river was full of algae in globular masses up to about an inch in diameter and occurring every few inches; they were covered with brown detritus but appeared to be healthy, and were certainly not confined to the surface.

The plankton was sampled with the silk net, which soon became completely clogged with these algae so that the catch was small, though it was probably fairly representative qualitatively. It contained:

Pisces : Engraulidae	2
Unidentified	1
Crustacea : Decapoda : <i>Penaeus</i> sp., young	A few
Cumacea	2
Amphipoda : small	1
Copepoda : including <i>Acartia lilljeborgi</i> Giesbr.	Many
Chaetognatha : <i>Sagitta</i> sp., small	"
Coelenterata : Scyphomedusae : <i>Stomolophus meleagris</i> , young	3
Ctenophora	1

Here again the presence of copepods seems to indicate unicellular plants on which they feed, this in spite of the great opacity of the water. The two cumaceans must represent a bottom fauna living in perpetual darkness. The occurrence of a ctenophore in water with a salinity as low as 13.9‰ is perhaps worth noting.

The abundance of living organisms in these Guiana estuaries is much greater than would be anticipated from the conditions of illumination, and a quantitative ecological study should prove of considerable interest. Many marine animals grow to a large size in the ocean abyss far below the region of active photosynthesis. They depend on the rain of food from the illuminated waters above. Similarly many of the animals described above from tropical rivers must have sought their food in the vegetable and animal detritus brought down from the rain forest and from more transparent inland waters.

B. GAMBIA RIVER, WEST AFRICA

Station 47: Nianimaru, 2.i.38

Nianimaru, where the river is nearly a kilometre wide, lies about 200 km. from the mouth of the Gambia river, which remains tidal for yet another 210 km. Even so the surface water was perfectly fresh, with a salinity of 0.00‰ just after high-water. The plankton, sampled with the silk net on the ebb, was of a fresh-water type, containing many reproducing cladocera, *Bosmina coregoni*, but nothing else. The 2-foot dredge, shot in 9 metres, came up full of mud devoid of anything living. The spectral absorption of the water was uniform and in no way remarkable. The depth of 1% illumination lay at 94 cm. so that the conditions for photosynthesis were much more favourable than in the Guiana rivers investigated, where the corresponding depths ranged from 22 to 40 cm. (see Table III).

TABLE III.—*Depth in metres at which total visible radiation was reduced to 1% of that incident on the surface. No correction for surface loss*

Station No.	Place	Depth m.
38B	Morowhana, Barima River	0.40
39	Jct. of Barima and Arouka Rivers	0.31
40	Demerara River, Georgetown	0.22
47B	Nianimaru, Gambia River	0.94
	Neal Point Buoy	0.3-2.2*

* The lower figure applies only for short periods near low water during wet weather in winter. For much of the year at this turbid station the depth of 1% illumination is likely to exceed 1.5 m.

TABLE IV.—*Depth in metres at which daylight factors of 80% and 60% would be found (corresponding to the zonal boundaries of Cooper & Milne (1939, revision of Table V, p. 395)*

Zonal boundary	I-II 80%	II-III 60%
Daylight factor		
Guiana rivers:		
Morowhana, Barima R.	0.0155	0.035
Jct. of Barima and Arouka	0.011	0.027
Demerara, Georgetown	0.010	0.024
Gambia River, Nianimaru	0.040	0.100
English estuary:		
Plymouth Sound	0.180	0.356
Hamoaze Buoys Nos. 4, 7 & 11	0.08-0.10	0.18-0.25

Station 48: Tendeba, 3.i.38.

Tendeba is some 120 km. below Nianimaru and about 80 km. from the mouth of the river. The surface salinity was 2.63‰ one hour after high-water. The plankton was sampled with the stramin net and appeared to be not markedly

more numerous than and definitely not so varied as in the much darker waters of the Barima river. The catch contained :

Pisces : Clupeidae : <i>Pellonula afzeliusi</i> Johnels	>200
" <i>Ilisha africana</i> (Bloch) 115-130 mm.	2
Sciaenidae : <i>Johnius elongatus</i> (Bowdich) 58-65 mm.	2
Atherinidae : Larvae, <15 mm.	>25
Crustacea : Decapoda : <i>Callinectes latimanus</i> Rathbun, ¹ female	1
<i>Penaeus</i> sp., immature	Many
Crangonidae, immature	"
Mysidacea	Abundant
Isopoda	1
Nematoda	1

¹ Several other crabs, presumably of this species and up to 10 cm. across, were seen at the surface drifting with the tide.

No copepods or *Sagittae* were caught, but they may have passed through the meshes of the net. The plankton at this station was remarkably colourless.

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SUMMARY

Waters from the tidal estuaries of the Rivers Barima and Demerara in British Guiana show extremely heavy absorption of light of all wave-lengths ; nevertheless, in spite of the unfavourable conditions for photosynthesis, the zooplankton is both varied and abundant. These observations in rivers of British Guiana are compared with similar ones made in the Gambia River, West Africa.

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